



Geographical origin of dabbling ducks wintering in Iberia: sex differences and implications for pair formation

MANUEL PAREJO,^{1*} JUAN G. NAVEDO,^{1,2} JORGE S. GUTIÉRREZ,^{1,3} JOSÉ M. ABAD-GÓMEZ,¹ AUXILIADORA VILLEGAS,¹ CASIMIRO CORBACHO,¹ JUAN M. SÁNCHEZ-GUZMÁN¹ & JOSÉ A. MASERO¹

¹Faculty of Sciences, Conservation Biology Research Group, Department of Anatomy, Cell Biology and Zoology, University of Extremadura, Badajoz 06006, Spain

²Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile

³Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, Den Burg, Texel 1790 AB, The Netherlands

Natural and anthropogenic Iberian wetlands in southern Europe are well known for supporting large numbers of migratory Palaearctic waterbirds each winter. However, information on the geographical origin of dabbling ducks overwintering in these wetlands is scarce and mostly limited to data from ringing recoveries. Here, we used intrinsic isotopic markers to determine the geographical origin of male and female Northern Pintails *Anas acuta* and Eurasian Teal *Anas crecca* in Extremadura, inland Iberia, a key site for overwintering dabbling ducks. Additionally, we fitted six Northern Pintails with GPS-GSM tags to complement the data derived from stable isotope analysis. Most (> 70%) first calendar-year Northern Pintails were assigned to regions above 55°N, flying 2600–5600 km from their main natal regions to Extremadura. Mean values of $\delta^2\text{H}_f$ varied significantly between male and female Northern Pintails, suggesting that the sexes had different geographical origins. Data from tagged adult Northern Pintails supported the isotopic data, one male flying more than 5000 km to the coast of the Pechora Sea (Russia). Most (> 70%) first calendar-year Eurasian Teal were assigned to the region between 48° and 60°N, travelling 1500–4500 km to arrive in Extremadura. Male and female Eurasian Teal showed marginal differences in mean values of $\delta^2\text{H}_f$. In migratory dabbling ducks, pairing typically occurs on the wintering grounds, and ducks in their first winter can breed the following spring. For Northern Pintails, pair formation in Extremadura could occur between individuals with different geographical origins, which could contribute to the genetic variability of their offspring.

Keywords: dabbling ducks, differential migration, natal origin, pair formation, stable isotopes.

The long-term stability of migratory bird populations is to a large extent determined by geographically separated events that occur during different periods of the annual cycle (reproduction, pre- and post-breeding migration and winter) (Newton 2008). Protecting migratory birds poses a great challenge, as they constitute more than 80% of avian species in temperate regions (Rappole 1995) and strongly influence ecosystem functioning (Wilcove

& Wikelski 2008, Bauer & Hoyer 2014). In this context, understanding how geographical connectivity influences the different stages of the annual cycle of migratory species is a central component of designing conservation strategies for such populations. For example, establishing geographical connectivity will help to predict how changes in the quality of breeding areas, stopover sites and/or wintering areas influence the migratory behaviour of birds (Martin *et al.* 2007, Reichlin *et al.* 2013).

Many populations of migratory waterbirds are declining (Mundkur & Nagy 2012), mainly due to

*Corresponding author.
Email: mparejonieto@unex.es

continuous loss and/or deterioration of natural wetlands (Rendón *et al.* 2008, Quesnelle *et al.* 2013). Iberian wetlands are among the main wintering areas for migratory Palaearctic waterfowl populations in Europe. Among these wetlands, the Doñana marshes, Ebro delta and Tagus estuary support large numbers of dabbling ducks (*Anas* spp.) (Scott & Rose 1996, Rendón *et al.* 2008, SEO/BirdLife 2012). Recently, other anthropogenic habitats such as rice fields and the reservoirs of Extremadura, inland Iberia, have emerged as key international sites for the populations of several dabbling ducks, such as Northern Pintail *Anas acuta* and Eurasian Teal *Anas crecca* (Navedo *et al.* 2012). Available information on the geographical origin of dabbling ducks in Iberia comes from ringing recovery data (SEO/BirdLife 2012). Previously available information on the geographical origin of Northern Pintails and Eurasian Teal wintering in Spain, based on historical records (1977–2011) of ringed bird recovery (SEO/BirdLife 2012), suggests that Northern Pintails mainly originate from Russia, Finland and Sweden, whereas Eurasian Teal come from Finland, the Netherlands, France and the UK. However, such information is sparse and can be biased by banding effort and/or hunting pressure in different geographical regions (Hobson 2011). The recovery rate of individuals of both species ringed in Spain during the winter (November to February) and recovered in other countries during the breeding season (May to August), and of birds ringed in other countries during the breeding season and recovered in Spain during the wintering season is very low: only two Northern Pintails and four Eurasian Teal were recovered during the last 30 years (1982–2012, data from Bird Migration Centre (CMA) of the Spanish Ornithological Society; www.anillamiento.seo.org).

In many species of migratory birds, males and females differ in some ecological aspects, such as the distance covered between the breeding and wintering grounds (Cristol *et al.* 1999, Newton 2008). Such sex-related differential migration also occurs among dabbling ducks, in which males typically migrate shorter distances than females (Perdeck & Clason 1983, Rodway 2007a,b, Newton 2008, Guillemain *et al.* 2009a). Understanding the geographical origin of males and females in the main wintering areas would therefore provide a range-wide perspective of migratory connectivity in dabbling ducks. As many waterfowl species pair

up in winter (Rohwer & Anderson 1988), patterns of gene flow and population structure might be defined during this period of the annual cycle (Robertson & Cooke 1999), so determining the geographical origin of the sex classes would also be useful to explain these patterns.

The measure of stable isotopes in feathers and other avian tissues has been shown to be a useful tool for determining migratory connectivity in numerous bird species (Hobson 2011). This tool is based on the existence of a relationship between the values of deuterium in the precipitation water at a geographical location ($\delta^2\text{H}_p$) and its incorporation into growing feathers or other tissues ($\delta^2\text{H}_f$) (Hobson 2011). The analysis of $\delta^2\text{H}$ of juvenile feathers grown in the breeding grounds and collected during winter can therefore be used to estimate the geographical origin of overwintering birds (Newton 2008). In Europe, several studies have used stable isotope analysis to determine the geographical origin of migratory birds sampled during winter (e.g. Bowen *et al.* 2005, Guillemain *et al.* 2013, Hobson *et al.* 2013a,b, Van Dijk *et al.* 2013). Furthermore, fine-scale methods such as global positioning systems (GPS) allow researchers to locate the spatial position of tagged individuals at discrete time intervals and enable the reconstruction of their migratory routes with more precision and accuracy than is possible with stable isotope analysis (Åkesson & Weimerskirch 2014, Willemoes *et al.* 2014).

The aim of this study was to assess the geographical origin of male and female Northern Pintails and Eurasian Teal overwintering in Extremadura. We analysed concentrations of $\delta^2\text{H}_f$ in juveniles of both species captured during the winter and tagged adult Northern Pintails with GPS-GSM transmitters to obtain additional information regarding their breeding grounds.

METHODS

Study site, species and capture

The anthropogenic wetlands of Extremadura (SW Spain) are a key site for many migratory waterbirds (Sánchez-Guzmán *et al.* 2007, Masero *et al.* 2009), including dabbling ducks (Navedo *et al.* 2012). Our study site was located at Vegas Altas del Guadiana (Fig. 1), where several large reservoirs provide roosting areas for waterbirds (Navedo *et al.* 2012). These reservoirs, together with

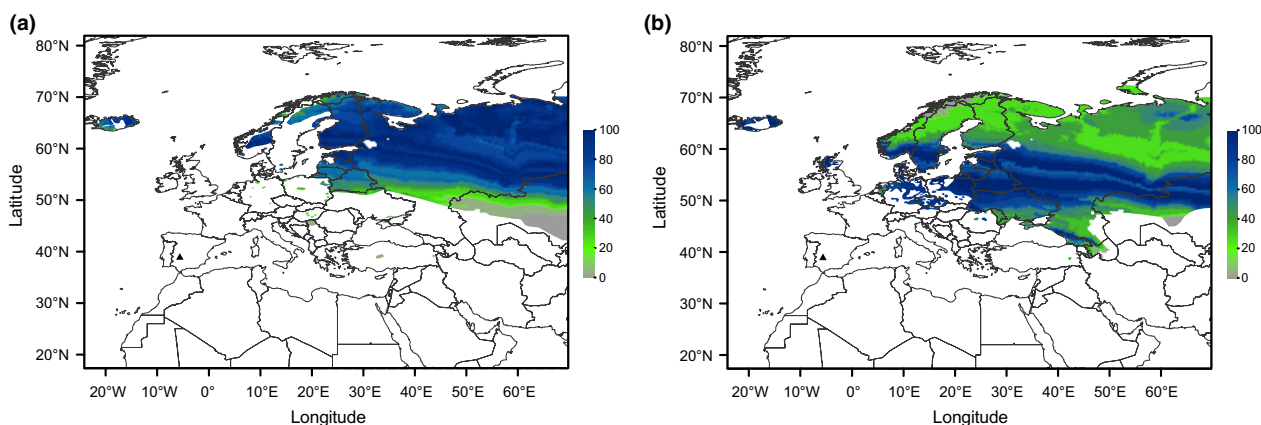


Figure 1. Geographical origin of first calendar-year (a) Northern Pintail and (b) Eurasian Teal (males and females combined) overwintering in Extremadura (▲). These maps represent the relative proportions of the individuals whose isotopic signatures ($\delta^2\text{H}_f$) matched the values of each cell of the isoscape within the European breeding range for each species, with a probability index of 2 : 1 (see Methods). The whole coloured area represents the potential breeding area according to the base maps provided by Birdlife International & NatureServe (2012). The correspondence between colour and origin probability for the population is shown in the legend inside the figures.

adjacent rice fields (25 000–30 000 ha), create an environmental mosaic that has promoted the populations of anatids and other wintering waterbirds in the area (Sánchez-Guzmán *et al.* 2007, Masero *et al.* 2011, Navedo *et al.* 2012).

The mean number of Northern Pintail and Eurasian Teal overwintering in Vegas Altas del Guadiana was 7235 and 9389 individuals, respectively (2007–2010, Navedo *et al.* 2012). During early winter (15 November to 31 December) 2008–2010, we captured juvenile individuals of both species using cannon nets. In total, we caught 24 Northern Pintail and 15 Eurasian Teal juveniles. Most individuals could be sexed and aged according to plumage characteristics. Nevertheless, we took a small blood sample from the brachial vein for molecular sexing (Santiago-Quesada *et al.* 2014).

Stable isotope analysis and assignment of geographical origin

In both species the outermost primary feathers were retained juvenile feathers (often contrasting in colour with inner primary and/or replaced secondary feathers) and so reflected the isotope ratios of natal origin. A small portion (< 0.5 cm) of the tip of the outermost primary feather was collected from each individual for the $\delta^2\text{H}_f$ analysis. Feathers were placed in labelled plastic bags and stored at $-30\text{ }^\circ\text{C}$ until further assay at the Iso-Analytical Laboratory (Cheshire, UK). Analyses were per-

formed using elemental analysis – isotope ratio mass spectrometry. Each feather was washed using sodium hydroxide solution and purified water, and oven-dried at $50\text{ }^\circ\text{C}$ for one night. Samples (1 mg each) were weighed into silver capsules, and filled capsules were left open (all samples at the same time) for a period of at least 4 days to allow the exchangeable hydrogen in the feather keratin to equilibrate fully with the moisture in the laboratory air (Wassenaar & Hobson 2003). Deuterium (D) values based on non-exchangeable hydrogen were expressed as the deviation (δ ; in parts-per-thousand) in the ratio of $^2\text{H}/^1\text{H}$, normalized according to the VSMOW-SLAP (Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation) scale using keratin isotope reference materials (mean \pm sd; BWB-II, whale baleen, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -108.00\text{‰}$, observed value = $-108.00 \pm 1.31\text{‰}$; IA-R002, mineral oil, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -111.20\text{‰}$, observed value = $-111.11 \pm 0.93\text{‰}$; IEA-CH-7, polyethylene foil, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -100.30\text{‰}$, observed value = $-101.42 \pm 1.13\text{‰}$; RSPB, eggshell membrane standard, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -99.0\text{‰}$, observed value = $-100.37 \pm 1.55\text{‰}$), which received identical times of exposure to laboratory air as feather samples. Each feather was measured in duplicate and the results are presented as mean values (repeatability was > 90%).

To assign the geographical origin of birds, we followed the protocol of van Wilgenburg and Hobson (2011). This approach provides a probability surface of areas consistent with potential origins. Information on the breeding distribution in the Western Palaearctic and the GIS-based model for $\delta^2\text{H}_p$ were extracted from the maps of the *Birds of the World* (Birdlife International & NatureServe 2012) and from Bowen *et al.* (2005), respectively. The latter was converted into $\delta^2\text{H}_f$ isoscape, following the equation $\delta^2\text{H}_f = -30.44 + 0.93 \delta^2\text{H}_p$, which accounts for 88% of the variance in $\delta^2\text{H}_f$ among anatids and passerines of known origin (Clark *et al.* 2006, 2009, Ashley *et al.* 2010). Mean values of $\delta^2\text{H}_f$ were extracted for the breeding ranges of each species using ARCGIS SPATIAL ANALYST. We assessed the probability that any given cell within the $\delta^2\text{H}_f$ isoscape represented the origin of an individual, using a normal probability density function:

$$f(y^*|\mu_c\sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right) \exp\left[-\frac{1}{\sqrt{2\pi}\sigma_c^2}(y^* - \mu_c)^2\right]$$

where $f(y^*|\mu_c\sigma_c)$ represents the probability that the cell (c) was the natal origin of an individual with an isotopic signature $\delta^2\text{H}_f(y^*)$, given the expected mean of $\delta^2\text{H}_f$ (i.e. isoscape prediction) for that cell (μ_c) and the expected standard deviation (σ_c) of $\delta^2\text{H}_f$ among individuals whose feathers grew in the same locations. Probability densities resulting from this equation were normalized, dividing the probability of a cell to be the origin of an individual between the sum of all the probabilities of the cells from where the individual might originate, to produce an origin probability map for each individual:

$$\pi_b = \frac{f(y^*|\mu_c\sigma_c)}{\sum_{b=1}^B f(y^*|\mu_c\sigma_c)}$$

To represent the origin of each sample, we converted the individual origin probability map, using a probability index 2 : 1 (odds ratio), considering the more probable origins against the more unlikely. Therefore, the region we assigned to each individual was twice as likely to be correct as the rest. We then selected the group of cells in the map that encompassed 67% of the origin probabilities; those cells were estimated and codified as 1,

whereas the remaining cells were codified as 0, to obtain a binary map for each individual. To obtain the origin probability for the population, the results of the assignment for each individual were grouped and represented in a $\delta^2\text{H}_f$ isoscape. All GIS analyses were performed using ARCGIS (ESRI, Redlands, CA, USA).

Transmitters

Six overwintering Northern Pintails (three adult males and three adult females) were cannon-netted and fitted with GPS-GSM tags (ECOTONE, model Duck 3). Transmitters were attached using a Teflon ribbon breast harness with a cotton weak link in the sternum. The weight of the transmitter was 35 g, thus being < 3.3% and 3.9% of the body mass of males and females, respectively. Transmitters recorded one GPS fix every 2 h and sent the data when five fixes were collected or when GSM coverage was reached, in areas with low or no GSM coverage.

Statistical analyses

We used a general linear model, with backward stepwise procedure, to test the effect of sex (fixed factor; two levels) on $\delta^2\text{H}_f$. Capture date (1 November = day 1) was included in the model as a covariate. Prior to analyses, data were examined for normality and homogeneity of variance. Analyses were performed using STATISTICA (version 10, Statsoft Inc., Tulsa, OK, USA). Throughout, two-tailed $P < 0.05$ was used as the level of significance.

RESULTS

$\delta^2\text{H}_f$ variation between sexes

Mean $\delta^2\text{H}_f$ values for male (-111.83 ± 10.72 , $n = 11$) and female (-100.72 ± 8.04 , $n = 13$) Northern Pintails were significantly different (sex: $F_{1,22} = 8.39$, $P < 0.01$). Mean $\delta^2\text{H}_f$ values for male (-97.7 ± 8.66 , $n = 9$) and female (-89.93 ± 7.03 , $n = 6$) Eurasian Teal did not differ significantly (sex: $F_{1,13} = 3.37$, $P = 0.09$). Date was dropped from the models ($P \geq 0.50$).

Geographical origin

According to the isotopic values, 90–100% of Northern Pintail juveniles overwintering in

Extremadura originated from the central and northeastern parts of their distribution in the Western Palaearctic (Fig. 1a). The geographical distribution of females ranged from 55° to 65°N (Fig. 2a), whereas males typically originated at higher latitudes, between 58° and 70°N, the northern part of the potential breeding range described for the species (Fig. 2c). Two of the three adult males equipped with transmitters completed migration: 'Pint 02' flew to the west coast of Denmark, near the locality of Højer (55°N), after covering 2342 km; and 'Pint 04' covered 5545 km to reach the coast of the Pechora Sea (Russia, above 68°N) (Fig. 3). In both cases, the individuals remained in those areas from 12 June to 1 October 2013. 'Pint 03' stopped transmitting when crossing the Swiss Alps (Fig. 3). Of the three tagged adult females, only one ('Pint 06') reached a potential breeding area close to the border between the Netherlands and Germany (near the town of Emden, 54°N; Fig. 3) after covering 2236 km. This individual remained there between

14 June and 27 July 2013. The other two tagged individuals, 'Pint 01' and 'Pint 05', were found dead along the coast of northern France and thus did not complete migration (Fig. 3).

For the Eurasian Teal, between 90 and 100% of the juvenile individuals came from the central parts of their breeding area in the Western Palaearctic, within the central part of the Volga river basin (Fig. 1b). The natal origin of females (probability 90–100%) ranged from 50° to 55°N (Fig. 2b), whereas that of males (probability 90–100%) ranged from 48° to 60°N (Fig. 2d).

DISCUSSION

Isotope analyses suggested that more than 70% of Northern Pintails that spent their first winter in Extremadura came from latitudes above 55°N. Most came from Fenno-Scandinavia as well as northern and central Russia, entailing a 2600–5600 km migration distance from the main breeding areas to the wintering grounds in Extremadura.

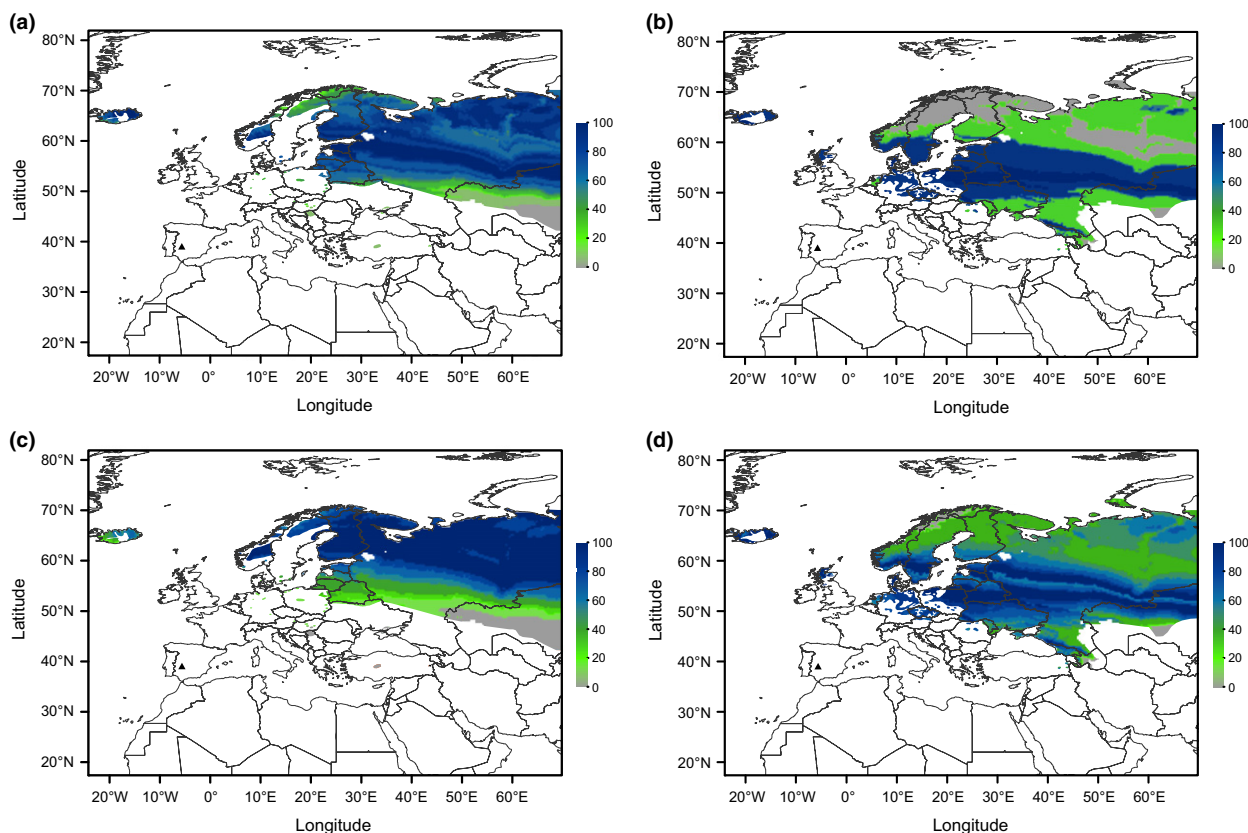


Figure 2. Geographical distributions for assigned origins for: (a) female Northern Pintails, (b) female Eurasian Teal, (c) male Northern Pintails and (d) male Eurasian Teal, captured between 2008 and 2010 in Extremadura (see the legend to Fig. 1).

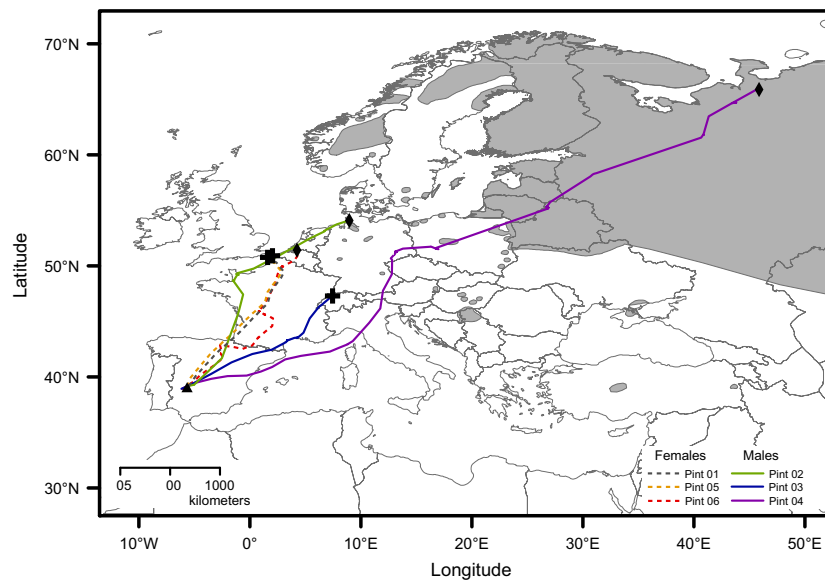


Figure 3. Migratory routes of three males (dashed lines) and three females (solid lines) equipped with GPS-GMS transmitters during the winter in Extremadura. The birds left Extremadura between 14 March and 2 May 2013; three of them died during northward migration (+) and the rest remained within the potential breeding areas between 12 June and 1 October 2013 (◆).

First-winter males in Extremadura came from breeding areas located further north than those of females. Therefore, areas such as the northern Scandinavian Peninsula or northern Russia represent the most probable origin of these males (80%), whereas the probability of females being born in those areas was 60%. The most probable origins of females (80%) were central Russia, Finnish Lapland and northern Iceland. Unfortunately, only three individuals with tags completed their migration (two males and one female). Despite the low sample size, our data show that male Northern Pintails can migrate more than 5000 km to reach their breeding areas. The two males migrated further north than the female, consistent with the pattern derived from the isotope analysis.

In North America and Japan, a large number of Northern Pintails have been marked with platform transmitter terminal (PTT) tags to study their migratory movements (Miller *et al.* 2005, 2010, Haukos *et al.* 2006). These studies have shown that they migrate long distances (over 4000 km during spring migration) but unfortunately there is no information on differential migration of males and females. In birds, there is increasing evidence that spatial segregation of sexes during the non-breeding season is a widespread phenomenon, and in many sexually dimorphic species, males (usually the larger sex) winter further north than females

(Newton 2008). Among migratory dabbling ducks, most species show differential migration, with males migrating shorter distances to winter further north than females (Rodway 2007a,b, Guillemain *et al.* 2009a and references therein). In the case of Northern Pintail, unfortunately, there are no published data on sex ratios in the main wintering sites through the East Atlantic flyway and other major flyways. Males and females overwintering in Extremadura come from different geographical breeding areas. Therefore, females of the same population as the overwintering males at Extremadura could spend the winter further south, in Doñana or West Africa, whereas males of the same geographical areas as females overwintering at Extremadura could winter further north, in France, the Netherlands or the UK.

There are three commonly (non-mutually exclusive) hypotheses to explain this sex-specific differential migration (Cristol *et al.* 1999, Newton 2008). The dominance hypothesis states that the socially dominant sex occupies better non-breeding habitat, forcing subordinates to migrate further or occupy less suitable habitats. The body-size hypothesis suggests that the larger sex usually winters at higher latitudes due to superior fasting endurance and thermal efficiency. The arrival-time hypothesis suggests that the sex that benefits most by arriving on the breeding grounds will minimize

migration distance. In migratory dabbling ducks, however, these hypotheses do not apply to most species due to their pairing behaviour during winter (see below) or fail to explain their differential migration (Guillemain *et al.* 2009a).

Over 70% of the wintering population of Eurasian Teal in Extremadura originates from 48° to 60°N, a biogeographical area located between central Europe and the Ural Mountains. The area where females most probably originate was narrower than that for males. Hence, more than 80% of the females originated from southeast Iceland, Denmark, northern Poland and central Russia, where in addition to these areas, males also come from northern Iceland, southern Norway, northern and southern Finland and north of the Russian Plain.

Recently, Guillemain *et al.* (2013) analysed the geographical origin of Eurasian Teal hunted in France using stable isotopes in feathers and recoveries of ringed birds, finding that Eurasian Teal wintering in France originated from areas further north in Europe (Finland to the Ural Mountains) than those wintering in Extremadura. Nevertheless, Eurasian Teal overwintering at Extremadura, France and the UK (Guillemain *et al.* 2009a,b, 2013) migrate similar distances between wintering and breeding areas (about 3100 km). Like Guillemain *et al.* (2005, 2013), we did not find sex differences in isotope ratios of Eurasian Teal overwintering at Extremadura.

Waterfowl are unusual in showing female-biased philopatry (Greenwood 1987, Anderson *et al.* 1992, Ely & Scribner 1994, Blums *et al.* 2002). Differences in the patterns of gene correlations for maternally inherited and nuclear genes have shown that females show greater natal philopatry than do males (Scribner *et al.* 2001, Liu *et al.* 2012). The acquisition of nutrient storage by pre-breeding females and arguments concerning the adaptive consequences of promoting or avoiding inbreeding have been proposed to explain these dispersal patterns and winter pairing (Rohwer & Anderson 1988, Chesser 1991a,b). It is known that many species of migratory waterfowl can breed 1 year after their birth (Rohwer & Anderson 1988), and thus pair formation can occur in Extremadura among juvenile Northern Pintails from distant geographical regions. This supports the possibility that winter pairing contributes to the avoidance of inbreeding. The level of genetic variation within Northern Pintail and other dabbling duck populations might result from gene

flow that is determined in the wintering grounds (Robertson & Cooke 1999, Scribner *et al.* 2001, Liu *et al.* 2013).

We show that, at least in the case of Northern Pintail, overwintering male and female juveniles in the south of Europe have different geographical origins. As pairing typically occurs on the wintering grounds, pair formation can occur among juvenile Northern Pintails from distant geographical regions, perhaps contributing to the avoidance of inbreeding. Further research is needed to assess the degree to which this pairing behaviour and migration strategy contribute to a higher degree of genetic variability.

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